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# REVISION AND REDEFINITION OF THE GENUS *RONDONANTHUS* HERZOG (ERIOCAULACEAE)<sup>1</sup>

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## ABSTRACT

The genus *Rondonanthus* Herzog has until now contained only the species *R. roraimae* and *R. micropetalus*, and has been defined by free petals in both sexes of flowers and the dioecious condition. It is here redefined according to a large suite of characters, especially the presence of long filamentous staminodes in the pistillate flowers, and by the adnation of the filament base to the corolla in the staminate flowers. Five additional species, including the monotypic genus *Wurdackia*, are transferred to *Rondonanthus*, and *R. micropetalus* is removed to *Paepalanthus*. It is proposed that *Rondonanthus* is a highly primitive paepalanthoid genus, to be taken as a primitive outgroup of *Syngonanthus*.

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The Eriocaulaceae are a pantropical monocot family of about 13 genera and 1,200 species (Kral, 1989). Except in rare cases, the flowers are unisexual and the plants monoecious, with the flowers borne in scapose heads.

Ruhland (1903) divided the family into two subfamilies, the Eriocauloideae, characterized by two whorls of stamens and a simple gynoecium, and the Paepalanthoideae, with a single whorl of stamens and vascularized secretory "appendages" inserted on the style alternate with the nonvascularized functional style branches. The Eriocauloideae are truly pantropical and contain many aquatic species, while the Paepalanthoideae are almost entirely limited to the New World (with some African disjuncts), and more xerophytic.

The Paepalanthoideae, which contain 11 of the 13 genera, have two centers of diversity, one in the Central Brazilian Plateau, especially the Cadeia do Espinhaço in Minas Gerais and Bahia, and one in the Guayana Highland, especially Venezuela. Botanical exploration of Guayana, in particular the tepui summits of Venezuela, has only been undertaken recently relative to that of the more accessible mountains of central Brazil, and has turned up many taxa of interest, including four endemic

paepalanthoid genera. These are *Rondonanthus* Herzog (1931), *Comanthera* Lyman B. Smith (1937), *Carptotepala* Mold. (1951), and *Wurdackia* Mold. (1957).

Following the lead of Ruhland (1903), all of these genera were described with reference to only a few floral characters. None contain more than two species, and none were discussed by their authors as to their relationships with other genera or implications for phylogeny. Recently, the availability of abundant collections from the Venezuelan tepuis and their study for Julian Steyermark's *Flora of the Venezuelan Guayana* (Hensold, in prep.) have acutely emphasized the need for study and reevaluation of these endemic genera.

In another work (Giuliatti & Hensold, 1991), we discuss the systematic position of *Comanthera* and *Carptotepala*, concluding that they are synonyms of *Syngonanthus* Ruhl. In this work, we find the genus *Rondonanthus* to be valid, though in need of redefinition, and include within it five additional endemic Guayanan species currently placed in three other genera, including the monotypic genus *Wurdackia*.

*Rondonanthus* as here recognized is a genus of great interest from the standpoint of phylogeny in

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Eriocaulaceae. It appears to combine characters of the Eriocauloideae with characters of two "core" paepalanthoid genera, *Paepalanthus* and *Syngonanthus*. As Stützel (1985) concluded (limiting his observations to *R. (Wurdackia) flabelliformis*), it appears to represent a primitive outgroup to the large genus *Syngonanthus*. As a genus, it also shows unusual variability with respect to certain floral characters, such as fusion of perianth parts and flower sexuality, which have until now been given a priori value in the definition of genera of Eriocaulaceae.

#### TAXONOMIC HISTORY

The genus *Rondonanthus* was described by Herzog (1931) on the basis of a single Luetzelburg collection of *R. roraimae* (Oliver) Herzog, based on *Paepalanthus roraimae* Oliver.

Herzog found only staminate flowers in his material and defined the genus by the free petals of the male corolla, which he believed to be unknown in *Paepalanthus*. Because he did not see the type material, he depended on Oliver's illustrations for his description of the pistillate flowers, which he described correctly as having the petals free and incorrectly as having simple style branches. Herzog also noted that the limited material he studied was dioecious and suggested this as an additional character of the genus, also encountered rarely in the family.

Ruhland (1903), in his comprehensive treatment of the family, had in fact erected *Paepalanthus* subg. *Bostrychophyllum* Ruhl. to accommodate *P. capillaceus* Klotzsch ex Koern., the single known species of *Paepalanthus* with free petals in the staminate flowers. This species is a vegetatively specialized submerged aquatic also native to Roraima, and is here treated as a species of *Rondonanthus*. (Ruhland had placed *P. roraimae* in "Species dubiae" since he had observed no material of the species.)

The same year that Herzog described *Rondonanthus*, Gleason (1931) described *Paepalanthus duidae* from Cerro Duida in Amazonas, noting the close similarity to *P. roraimae* Oliver, and differentiating it from that species only by minor characters of gross morphology, and without mention of floral structure.

Later, additional species of *Rondonanthus* were described from the Chimantá Massif and placed in *Syngonanthus* (*S. acopanensis* Mold., 1948, and *S. obtusifolius* Mold., 1957), and in a new monotypic genus *Wurdackia* (*W. flabelliformis* Mold., 1957). All exhibit typical *Syngonanthus*-like co-

rollas, with the corollas of the staminate flowers tubular and those of the pistillate flowers connate at the middle and free at the base and the apex. *Wurdackia*, however, differed in being the first known species of the family with bisexual flowers.

All of these taxa are here treated in *Rondonanthus*, though their differences in corolla fusion characteristics and flower sexuality originally caused them to be assigned to four different genera.

The only other species described in *Rondonanthus* since the type species, *R. micropetalus* Mold. (1951), reputedly with free petals in the staminate flowers, is here removed to synonymy in *Paepalanthus* Ruhl. (see Excluded Species).

#### GENERIC DEFINITION AND AFFINITIES

The single character that best distinguishes *Rondonanthus* from all other genera of Eriocaulaceae is the presence of long linear staminodes in the pistillate flowers. Staminodes are known in *Paepalanthus*, but they are small and scalelike, never linear. The only species of *Rondonanthus* in which these are not found is *R. flabelliformis*, in which they are replaced by functional stamens which produce and release pollen in apparently normal quantities.

*Rondonanthus* is further defined by a mixture of characters individually found in other genera, especially *Syngonanthus* and *Paepalanthus*, but not in combination with each other.

The affinities of *Rondonanthus* appear to lie most closely with *Syngonanthus*, for a number of reasons. In *R. acopanensis*, *R. caulescens*, and *R. flabelliformis*, the petals of the pistillate flowers are fused in the middle but free at the base and apex, which is considered to be one of the defining characters of *Syngonanthus*. Elsewhere in the Eriocaulaceae, this is known only in the genus *Philodice* C. Martius (2 spp.), which is considered to be derived from *Syngonanthus*, and in *Mesanthemum* Koern., which with two whorls of stamens and an unmodified gynoeceum is quite distant from *Rondonanthus*.

This character, however, is not stable in the genus. In *R. roraimae* and *R. capillaceus*, the petals of the pistillate flowers are always free, and in the variable species *R. duidae*, most populations have free petals, but a single population has been found (at Aprada-tepui) with brief petal fusion. In the genus *Syngonanthus*, the character also shows a small degree of instability. In the reduced, dimorous species *S. minutus* (Mold.) Hensold (1991), for example, the petals are free, and this situation is also occasionally found in sect. *Thysanocephalus*

(Koern.) Ruhl., as in *S. jenmanii* (Gleason) Giulietti & Hensold (1991). Petal fusion probably represents a primitive state in *Rondonanthus*, as is also considered to be the case in *Syngonanthus*.

Fusion of the corollas of the staminate flowers is a fairly universal condition in the Paepalanthoideae, but this character also breaks down in *Rondonanthus*. Of the species with free petals in the pistillate flowers, *R. capillaceus* also has free petals in the staminate flowers, *R. roraimae* has petals connate early in development and then separating, and *R. duidae*, except in very rare cases, has petals persistently connate. The remaining three species, which all exhibit fusion of corollas in the pistillate flowers, similarly have fused corollas of the staminate flowers.

Other characters which indicate an alliance with *Syngonanthus* are the following: roots pale and aerenchymatous; hairs present on the floral axis at ovary base; base color of the perianth creamy white; pubescence of malpighian hairs on vegetative parts. All of these characters except the last may also be found in the genus *Leiothrix* Ruhl., but this genus is differentiated by specialized morphology of the gynoecium, seed testa striations, and basifixed anthers (Giulietti, 1984).

Stützel (1988) found similar root anatomical structure in *R. roraimae*, *Syngonanthus* (*Carpototepala*) *jenmanii* (sect. *Thysanocephalus*), and *Mesanthemum*. A divergent type of aerenchymatous morphology was observed in *S. chrysanthus* (Bong.) Ruhl. (sect. *Dimorphocaulon* Ruhl.), *S. caulescens* (Poiret) Ruhl. (sect. *Carphocephalus* Ruhl.), and *Philodice*.

Aerenchymatous roots are unknown in the genus *Paepalanthus*, however, and we also have never observed malpighian hairs in this group. The presence of hairs at the base of the ovary is a character that has not been systematically surveyed in the family but which we have not encountered in *Paepalanthus*. The white base color of the perianth and often also the involucre bracts is a conspicuously common character in *Syngonanthus*, but probably rare (if at all present) in *Paepalanthus*.

On the other hand, a number of other characters occur in *Rondonanthus* which are much more commonly observed in *Paepalanthus*. The most notable is the deeply bifid style branches found in all species of *Rondonanthus* and in most *Paepalanthus*, but never described from *Syngonanthus* or *Leiothrix*.

Certain characteristics are shared by *Rondonanthus* with *Paepalanthus* and also the putatively more primitive Eriocauloideae (*Eriocaulon* L. and *Mesanthemum*). These are: the opaque blackish

coloration of the involucre bracts, and frequently also the upper parts of the perianth; the tufts of trichomes on the tips of the sepals and floral bracts; the clavate or subclavate shape of these perianth trichomes, which sometimes (*R. capillaceus*) are densely ornamented on the internal wall; and, in three species, the ciliate margins of the staminate flower corollas.

All of these characteristics are common in the Eriocauloideae. The last is not known from any species of *Syngonanthus*, but is common in some of the less specialized members of *Paepalanthus*, notably subg. *Xeractis*. Inner wall ornamentation in floral trichomes has also not been described from *Syngonanthus* but is the rule in *Paepalanthus*. Bearded sepal apices are known in *Syngonanthus* (especially in sect. *Dimorphocaulon*, e.g., *S. humboldtii* (Kunth) Ruhl., *S. diamantinensis* Silveira), but not common, and involucre bract pigmentation, when it occurs, is usually more or less translucent and reddish (*S. arenarius* (Gardner) Ruhl., *S. anomalus* (Koern.) Ruhl.). An exception is *S. niger* Silveira, with long black linear-lanceolate bracts.

Furthermore, in *R. acopanensis*, the outermost bracts, as well as the inner bract apices, are apparently green and leaflike when young, which may be interpreted as a lack of specialization. This same situation is also found in some species of *Paepalanthus* subg. *Xeractis* Koern. (*P. digitiformis* Hensold, *P. dianthoides* Koern.).

Thus, certain parallels can be drawn between *Rondonanthus* and *Paepalanthus* subg. *Xeractis*, which are both interpreted as primitive within their respective lineages (Hensold, 1988). Both possess, in their less specialized species, lanceolate, leaflike bracts which surpass the head. In subg. *Xeractis* these bracts are commonly pubescent on the inner surface, and this is also found occasionally in *Rondonanthus*, as also in *Mesanthemum*. Both also have typically pilose corollas of the staminate flowers, though this is also an extremely rare characteristic elsewhere in the Paepalanthoideae, known only in a few species of *Paepalanthus* closely related to subg. *Xeractis*.

Another exceptional character of *Rondonanthus* is the fusion of the filament base with the corolla. This occurs in four of the five species of *Rondonanthus*. (In *R. capillaceus*, the only species in the genus with an "androphore," or elongated floral axis above the sepals, the petals are inserted at the base of the androphore while the stamens are inserted at its apex, and therefore adnation of the filaments is impossible.) Adnate filaments are common in the Eriocauloideae (both

*Eriocaulon* and *Mesanthemum*) but not heretofore documented in the Paepalanthoideae. (We have also found them to occur in *Syngonanthus* sect. *Carphocephalus* and in *S. amazonicus* Mold.)

#### IMPLICATIONS FOR PHYLOGENY

*Rondonanthus* thus combines characteristics of the Eriocauloideae, *Paepalanthus* and *Syngonanthus*. It apparently has strong affinities to *Syngonanthus* but differs from that genus in characters that seem more primitive in the subfamily or family as a whole. Moreover, it presents variation in flower sexuality, fusion of the petals, and presence of trichome wall thickenings, all characters which have been used to define genera.

Stützel (1985), studying *R. (Wurdackia) flabelliformis*, posited it as an "evolutionary link" between *Syngonanthus* and *Mesanthemum*. *Mesanthemum* also shows *Syngonanthus*-like fusion of the pistillate flower corolla, but like *Eriocaulon* possesses two whorls of stamens and an unmodified gynoecium. As evidence, Stützel cited (a) the bifid style branches of *Wurdackia*, which he interpreted as primitive relative to the simple style branches of *Syngonanthus*; and (b) the adnation of the filaments to the corolla shared by "*Wurdackia*" and *Mesanthemum*, but believed by him to be lacking in *Syngonanthus*.

Stützel did not consider the bisexual flower of "*Wurdackia*" to represent a necessarily primitive state, observing that in eriocauls differentiation of floral sexuality occurs late in development (Stützel, 1985) and might be readily subject to evolutionary modification. Having found that (1) bisexual flowers occur together with staminate flowers in the same head; (2) "*Wurdackia*" has very close sympatric relatives with normal pistillate and staminate flowers; and (3) these related species possess long filamentlike staminodes in the pistillate flowers, we agree that the bisexual flowers of "*Wurdackia*" are probably secondarily derived.

In the same publication, Stützel (1985) proposed a new three-subfamily system of classification for the Eriocaulaceae, in which the Syngonanthoideae (*Mesanthemum*, *Wurdackia*, *Syngonanthus*, and *Philodice*) and the Paepalanthoideae s. str. (*Paepalanthus*, *Lachnocaulon* Kunth, *Tonina* Aublet, *Blastocaulon* Ruhl., and *Rondonanthus*) are independently derived from the Eriocauloideae, containing only *Eriocaulon*.

*Rondonanthus* (represented only by *R. roraimae*) was evidently placed in the Paepalanthoideae because of the free petals in the pistillate flowers. The union of *Wurdackia* with *Rondonanthus*,

however, does not create problems for Stützel's phylogeny, especially if we suppose that free petals are a derived character in the genus. In addition, the styles of *Rondonanthus* s.l. are shown to be bifid, rather than simple, and the filaments adnate to the corolla, all of which characters are compatible with Stützel's system.

This three-subfamily system is problematic, however, not in its phylogenetic interpretation of "*Wurdackia*," but in the cladistic emphasis it places on "syngonanthoid" fusion of the pistillate flower corolla. Stützel cited scanning electron microscope (SEM) developmental studies of flowers (Stützel, 1984) which have revealed the pistillate flower corolla of *Syngonanthus* to be congenitally fused, while that of *Paepalanthus* is shown to be congenitally free. He concluded that the flowers of *Paepalanthus* cannot be derived phylogenetically from those of *Syngonanthus*, and that the genus must therefore have a separate origin in the Eriocauloideae, perhaps in *Eriocaulon*, in which petals of both sexes of flowers are free.

This classification, however, assumes that evolution of the highly modified gynoecium with its "stylar appendages," not to mention the reduction of stamens from two whorls to one, must occur twice in evolution. The alternative is to assume either that (a) the syngonanthoid corolla arose twice in separate lines, or (b) *Paepalanthus* was originally derived from a species with a syngonanthoid corolla, in spite of the lack of ontogenetic evidence.

The first alternative does not seem unlikely, especially in view of the finding that corolla fusion is a character showing much less stability, especially in the primitive genus *Rondonanthus*, than that of gynoecial modification. The paepalanthoid gynoecium furthermore must be thought of as involving more than one major evolutionary change, i.e., the modification of the ancestral style into an "appendage" (nectary) and the formation of non-vascularized functional styles at a position rotated 60 degrees from the position of the original styles. As far as we know there are no intermediate forms in existence, and no cases in the Paepalanthoideae where the gynoecium has reverted to the primitive state. The second alternative is also not hard to visualize, if we do not assume that ontogeny faultlessly recapitulates phylogeny.

We agree that *Syngonanthus* and its allies seem to constitute a natural group which may be usefully distinguished from *Paepalanthus* and its allies. What is most necessary at present is to survey the subgenera and sections of these two large, polymorphous, and probably unnatural genera in an effort to better characterize the taxa involved and

to more fully identify and survey characters of evident taxonomic importance.

Moreover, if *Rondonanthus* is taken as a primitive outgroup of *Syngonanthus*, it may aid in the assessment of whether *Syngonanthus* is mono- or polyphyletic, and if the latter, how it is to be properly divided to reflect phylogeny.

We feel it is more practical and parsimonious to retain for the present Ruhland's two-subfamily classification while acknowledging that much more information is needed to build a strong phylogenetic understanding of Eriocaulaceae.

#### TAXONOMY

**Rondonanthus** Herzog, Feddes Repert. Spec. Nov. Regni Veg. 29: 210. 1931. TYPE: *Rondonanthus roraimae* (Oliver) Herzog.

*Wurdackia* Mold., Mem. New York Bot. Gard. 9: 413. 1957. TYPE: *Wurdackia flabelliformis* Mold.

*Paepalanthus* subg. *Bostrychophyllum* Ruhl., Pflanzenr. IV. 30: 220. 1903. TYPE: *Paepalanthus capillaceus* Klotzsch ex Koern.

Plants rosulate or caulescent cespitose perennials branching at ground level. Roots creamy white to pale brown, porous (aerenchymatous), brittle, not spongy, usually sparingly branched, the branches evidently much smaller in diameter than main roots. Stems ca. 2–10 mm diam., woolly with fine cream to tan-colored filamentous hairs. Leaves spirally arranged or distichous, filiform to linear or ligulate, the young leaves attaining full width long before full length; the bases also with parallel margins, but dilated with respect to the blades, at least distally, somewhat scarious and frequently woolly with hairs like those of the stem. Pubescence of leaves and peduncles when present mostly a mixture of filamentous and malpighian hairs, the latter usually "retorse" (i.e., strongly asymmetric with the larger end proximal); capitate hairs lacking. Inflorescences single to numerous per age class and then usually  $\pm$  synchronous. Peduncle sheaths  $\pm$  membranous with respect to the leaves, often pale and scarious at least toward the upper margin, closed over the young inflorescences and splitting down one side from just below the apex, the opening oblique with the upper margins remaining minutely involute and often eventually lacerate. Peduncles mostly 3- or 6-costate, sometimes apparently more. Capitula turbinate to hemispheric at maturity, rarely subglobose. Involucral bracts, or at least their visible apices, triangular to lanceolate, acute to subacute, gold to nearly black, or variegated. Receptacle pilose. Floral bracts present, usually about equaling the flowers, linear to spatulate, pubescent

abaxially at apex. Flowers 3-merous, either staminate and pistillate or staminate and bisexual, the two types usually found in different zones in the same capitulum or rarely (*R. roraimae*) most capitula and plants unisexual. *Staminate flowers*. Pedicels 0.3–2.5 mm, sometimes equaling or even exceeding the flowers in length. Sepals free, elliptic to spatulate, pubescent abaxially at apex. Petals free or connate into a 3-lobed tube, and then sometimes separating after anthesis, glabrous or pilose at upper margin. Androphore usually lacking; when present, the petals free and borne at its base. Stamens adnate to corolla at base, except when separated from corolla by androphore; anthers dorsifixed, white or cream. *Pistillate and bisexual flowers*. Pedicels 0.2–2.0 mm long. Sepals free, ovate to elliptic to spatulate, pigmented as in the staminate flowers or lighter, pubescent as in the staminate flowers, expanding and thickening with maturation of the fruit, especially at base. Petals free or connate distally and free at the base, glabrous or pilose at upper margin and abaxially. Linear staminodes, or more rarely fully developed stamens, present opposite petals, the staminodes usually about half to twice the height of the ovary and bearing two tiny brownish lobes at the apex. Ovary usually subtended by a ring of long hairs, the style much shorter than the style branches; the appendages infundibular, stalked, papillose, inserted on style at or commonly slightly below the level of divergence of the style branches; the style branches strongly bifid. Fruit a loculicidal capsule. Seeds ellipsoidal, reticulate, the longitudinal striations of the testa raised and more conspicuous than the transverse. Floral trichomes subacute to subclavate, with or without granular thickenings of the internal wall.

#### KEY TO THE SPECIES OF *RONDONANTHUS*

- 1a. Plants submerged aquatics; leaves filiform-septate, usually surpassing the peduncles; heads 3–5 mm diam.; floral bracts and sepals short-hairy ..... *R. capillaceus*
- 1b. Plants terrestrial; leaves linear to ligulate, always surpassed by peduncles; heads 6–19 mm diam.; floral bracts and sepals densely bearded with long hairs.
  - 2a. Leaves distichous.
    - 3a. Stems leafy to base; flowers bisexual and staminate ..... *R. flabelliformis*
    - 3b. Stems leafy only at apex; flowers pistillate and staminate ..... *R. acopanensis*
  - 2b. Leaves spirally arranged.
    - 4a. Peduncles 3-costate; involucral bracts of upper series acuminate, the acumens colorless ..... *R. caulescens*
    - 4b. Peduncles 6-costate; involucral bracts of upper series subacute to acute, black

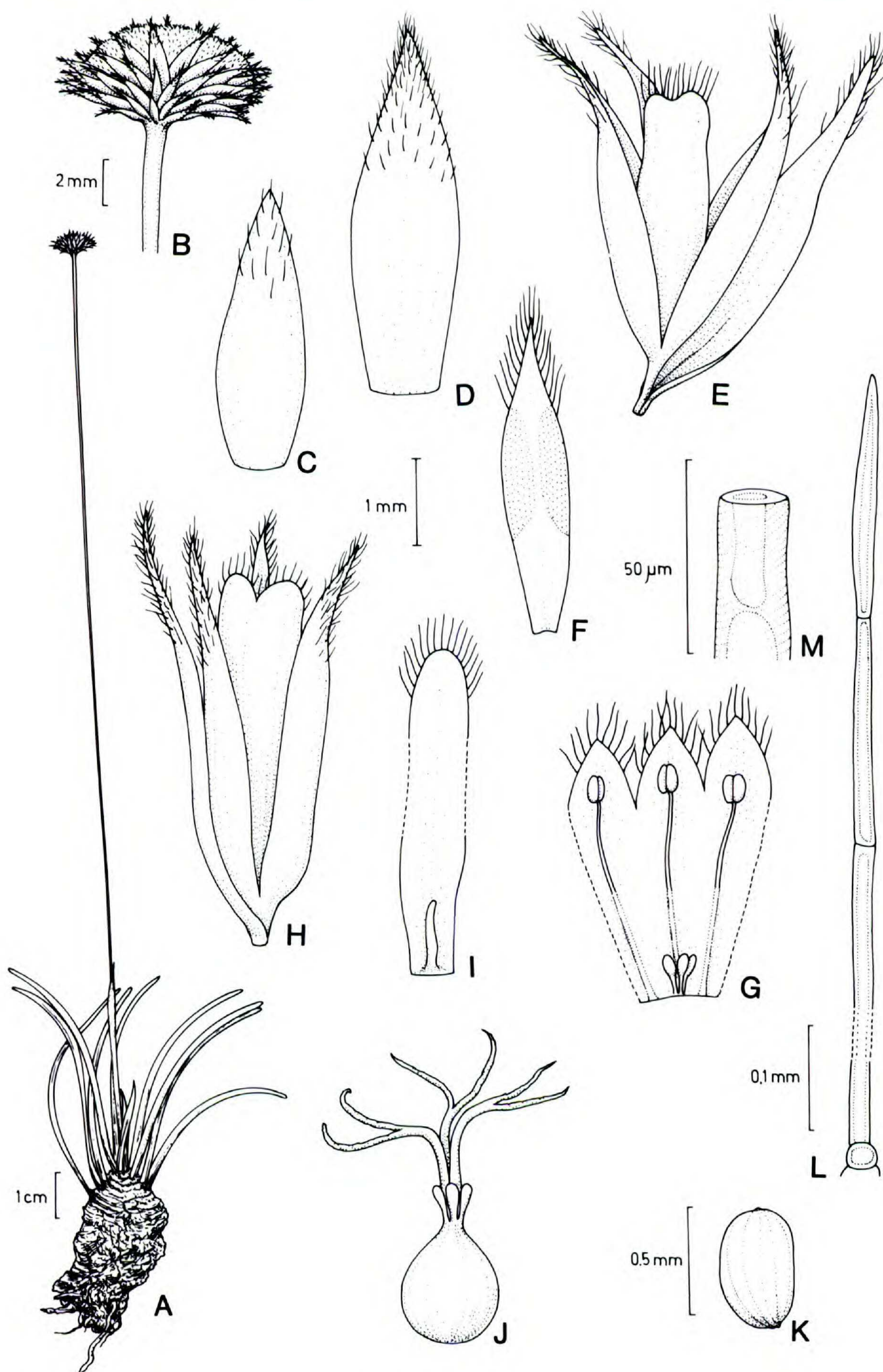


FIGURE 1. *Rondonanthus acopanensis* (Mold.) Hensold & Giulietti var. *acopanensis* (Steyermark 128872 MO).—A. Habit.—B. Inflorescence.—C, D. Involucral bracts. E–G. Staminate flower.—E. Flower with bract, past anthesis (corolla involute at upper margin).—F. Sepal, adaxial view.—G. Corolla tube, opened to show stamens and pistillodes. H, I. Pistillate flower.—H. Flower with bract, past anthesis.—I. Petal, with hatched lines showing where fused with adjacent petal, and staminode adhering at base.—J. Gynoecium (fruiting).—K. Seed.—L, M. Trichome of floral bract apex.

- at apex and margins, though sometimes the midvein pale.
- 5a. Leaves sharp-cuspidate to aristate; petals of staminate flowers persistently connate and ciliate at upper margin ..... *R. duidae*
- 5b. Leaves obtuse to subacute; petals of staminate flowers connate early but separating by anthesis, glabrous ..... *R. roraimae*

***Rondonanthus acopanensis*** (Mold.) Hensold & Giulietti, comb. nov. *Syngonanthus acopanensis* Mold., *Phytologia* 3: 41. 1948. TYPE: Venezuela. Bolívar: Chimantá Massif, Cerro Acopán, 1,900 m, *Cardona* 2280 (holotype, US; isotype, NY). Figure 1.

Plants short-stemmed caespitose perennials. Main roots ca. 0.5–1.2 mm diam., sparingly branched, cream to pale orange-brown. Stems 1–4 cm long at flowering, ca. 2–5 mm diam., leafy only near apex, but the lower portions covered with tightly persistent flabelliform leaf bases (these making the stem appear laterally compressed and 5–20 mm wide), woolly with cream-colored hairs. Leaves distichous, 3–13 cm long, 1–4(–6) mm wide, the base and blade abruptly differentiated, the base linear, dilated with respect to blade, scarious, densely enfolded with long cream-colored woolly hairs (often black with dirt), and persistent, a transverse abscission layer apparently forming at the juncture with the blade; the blades linear, subacute to broadly rounded or truncate depending on width, cartilaginous and rigid, glabrous or pubescent with retrorse malpighian hairs when young especially adaxially, 5–30-veined, the veins of equal size. Inflorescences single per age class, the old ones often persistent on stem. Peduncle sheaths 2–11 cm long, twisted, mostly striate-pubescent with retrorse malpighian hairs, the apex acute to rounded (corresponding in shape to leaf apex), green or scarious, frequently lacerate with age. Peduncles 12–45(–60) cm long, 6-costate, sometimes apparently more by division, pubescent with retrorse malpighian hairs and long filamentous hairs fringing the base of the capitulum. Capitula 7.5–12(–15) mm diam., turbinate to hemispheric at maturity. Involucral bracts in 3–5 series, the outer narrowly triangular to lance-linear, subacute to acute, erect to slightly recurved-spreading, 2.5–5.5 mm long, 0.6–1.0 mm wide at base, the inner bracts oblanceolate, broadly acuminate, erect, 4–7 mm long, 0.8–1.3 mm wide, mostly surpassing the head by ca. 0.5–1.5 mm; the outer bracts pale brown to castaneous, or greenish when fresh, the inner black except for the pale tip and midvein; the outer bracts

usually ciliate and hirsute abaxially, the inner densely bearded at the apex, at least abaxially and sometimes also adaxially, glabrate with age. Floral bracts commonly exceeding the flowers, linear to linear-oblong, acuminate, sometimes with a long “whip tip,” blackened distally, tufted with hairs abaxially at apex. *Staminate flowers*. Pedicels 0.7–1.3 mm long. Sepals obovate-elliptic to spatulate, attenuate-acute to long-acuminate, 2.3–3.5(–4.0) mm long, 0.6–0.9 mm wide, white at base, blackened distally except for white midvein and apex, the apex tufted abaxially with divergent trichomes like a bottlebrush. Corolla connate into a 3-lobed tube, the androphore lacking, the tube 2.0–3.5(–4.5) mm long, the lobes triangular-obtuse, the upper margin and abaxial lobe apices ciliate-pilose, involute and retracting the stamens after anthesis. Stamens with filaments adnate to corolla at base,  $\pm$  included; anthers ca. 0.3–0.35 mm long. *Pistillate flowers*. Pedicels 0.6–0.8 mm long. Sepals elliptic to ovate-elliptic, concave, acuminate, 3.5–4.0(–4.7) mm long, 1.0–1.5 mm wide, cream-colored or pigmented as in staminate flowers though usually more weakly so, tufted at the apex as in the staminate flowers, thickening at base at maturity. Petals connate into a tube except at base, the segments oblong,  $\pm$  rounded at apex, 2.8–3.5(–4.7) mm long, 0.6–0.9 mm wide, densely ciliate at upper margin and frequently also pilose abaxially at apex or in submarginal bands. Stamines linear, 0.6–1.3(–2.5) mm long. Ovary ringed by hairs at base, 0.4–0.7 mm long, the style 0–0.3 mm long, the appendages ca. 0.4 mm long, the stalk thick, the papillose portion orange-brown, the style branches diverging slightly above the appendages, 1.5–2.3 mm long, conspicuously bifid. Floral trichomes subacute to rounded, lacking granular thickenings of the internal wall.

This species is endemic to the Chimantá Massif in Bolívar, Venezuela, where it is represented by two sympatric varieties, heretofore recognized as species. They are about equally commonly collected and are distinguishable only by their size and robustness, as well as possible habitat differences. This sort of variation crops up not uncommonly in eriocauls (as in *Paepalanthus superbus* Ruhl. and *P. chlorocephalus* Silveira in the Serra do Cipó, Brazil; Hensold, 1988), and is possibly associated with polyploidy or some other macromutation. This would imply that the larger form may be “polyphyletic,” having been derived several times from the smaller form. (An alternative view would be that the smaller form may have been derived from the larger form.) However, because we lack cytological data, and since each type is

about equally widespread and forming uniform populations, we have treated them as varieties.

- 1a. Leaves 1–2 mm wide; heads 7.5–10 mm diam.; involucre bracts mostly ca. 3-seriate .....  
..... *Rondonanthus acopanensis* var. *acopanensis*  
1b. Leaves (2–)2.8–6 mm wide; heads 10–14(–15) mm diam.; involucre bracts mostly ca. 4–5-seriate .....  
..... *Rondonanthus acopanensis* var. *obtusifolius*

### ***Rondonanthus acopanensis* var. *acopanensis***

Stems, including attached leaf bases, ca. 5–10 mm wide. Leaves 1–2 mm wide, 5–7(–9)-nerved, firm, green, subacute, the margins not turning shiny brown. Heads 7.5–10 mm diam. Involucre bracts in 3 series, the lowest lanceolate, 2.5–3.5 mm long, 0.6–0.9 mm wide. Floral bracts 3.5–4.7 mm long. Staminate flowers with sepals 2.3–3.3 mm long, 0.6–0.8 mm wide, and corollas 2.0–2.7 mm long. Pistillate flowers with sepals 3.5–4.0 mm long, 1.0–1.4 mm wide, and corollas 2.8–3.2 mm long.

*Phenology.* Collected in flower mostly from January to March, but also occasionally in June and August.

*Habitat and distribution.* Locally abundant on wet sandy depressions and banks on shallow soils, in the open or in scrub forest, 1,900–2,600 m. Venezuela. Bolívar: Chimantá Massif (Acopán-, Apácará-, Chimantá-, Murey- (Eruoda-)tepuis).

*Additional specimens examined.* VENEZUELA. BOLÍVAR: Chimantá Massif, Apácará-tepui, N section, *Huber & Colella* 8685 (LL, NY, VEN), *Huber & Colella* 8737 (LL, NY); Apácará-tepui, E-central section, *Steyermark* 75925 (F); Apácará-tepui, S section, *Huber & Steyermark* 6964 (LL, MO), *Huber & Steyermark* 6970 (LL); Apácará-tepui, SE section, *Steyermark* 75850 (F); Chimantá Massif, Murey- (Eruoda-)tepui, *Huber* 11575 (NY), *Steyermark* 115818-A (LL, VEN); Chimantá Massif, Chimantá-tepui, central-NE sector, *Steyermark et al.* 128165 (LL, MO, NY, VEN); Chimantá-tepui, E sector, vicinity of Caño del Grillo, *Huber & Steyermark* 7160 (LL, MO), *Steyermark & Wurdack* 804 (F, NY), *Steyermark* 128872 (LL, MO), *Steyermark* 128938 (LL); Chimantá Massif, Churi-tepui, *Wurdack* 34213 (F, NY, VEN), central-SE section, *Huber & Colella* 8934 (LL, NY), *Huber* 9275 (MO); Angasima-tepui, 10 km SE of Chimantá Massif, *Huber* 11688 (MO).

### ***Rondonanthus acopanensis* var. *obtusifolius***

(Mold.) Hensold & Giulietti, comb. et stat. nov. *Syngonanthus obtusifolius* Mold., Mem. New York Bot. Gard. 9: 410. 1957. TYPE: Venezuela. Bolívar: Chimantá Massif, central section, 1,940 m, 4 Feb. 1955, *Steyermark & Wurdack* 406 (holotype, NY; isotypes, F, GH).

Stems, including attached leaf bases, ca. 12–20 mm wide. Leaves (2–)2.8–6 mm wide, ca. 11–19(–30)-nerved, rounded to nearly truncate, very firm-coriaceous (only firmly chartaceous in *Huber* 11522), the margins, especially near the apex, often shiny and deep brown-tinged. Heads 10–14(–15) mm diam. Involucre bracts in (3–)4–5 series, the lowest lance-linear, ca. 3.5–6 mm long, 0.7–1.0 mm wide. Floral bracts 3.5–6.2 mm long. Male flowers with sepals 3.0–3.5(–4.0) mm long, 0.6–0.9 mm wide, corolla 3.0–3.5(–4.5) mm long. Female flowers with sepals ca. 3.5(–4.7) mm long, ca. 1.3–1.5 mm wide, corolla 3.0–3.5(–4.7) mm long.

*Phenology.* Collected in flower late January to mid-March.

*Habitat and distribution.* Locally abundant in open wet savanna and among sandstone outcrops, at 1,800–2,200 m. Venezuela. Bolívar: Chimantá Massif (Abacapá-, Acopán-, Apácará-, and Chimantá-tepuis).

*Additional specimens examined.* VENEZUELA. BOLÍVAR: Chimantá Massif, Apácará-tepui, S sector, *Huber & Steyermark* 7061 (LL, NY), *Steyermark* 128428 (LL, MO), *Steyermark et al.* 128519 (LL, MO); Apácará-tepui, SE sector, *Huber et al.* 8854 (LL, NY), *Huber et al.* 8878 (LL, NY), *Huber* 11522 (MO), *Huber* 11524 (NY); Chimantá-tepui, NE sector, *Huber & Steyermark* 6864 (LL, NY); Chimantá-tepui, central-NE sector, *Steyermark et al.* 128090 (NY, MO); Chimantá-tepui, central-S sector, *Huber et al.* 10179 (MO); Abacapá-tepui, S sector, *Huber & Dezzio* 8620 (NY); Acopán-tepui, W sector (Amurí-tepui), *Huber & Steyermark* 7082 (LL, VEN), *Steyermark et al.* 128453 (LL, MO), *Steyermark et al.* 128793 (LL); Acopán-tepui, NE sector, *Huber et al.* 10152 (NY), SE sector, *Huber* 9065 (LL, NY), SSE sector, *Steyermark et al.* 129909 (LL, VEN).

The specimen *Huber* 11522 is included here with some reservation. It differs from typical var. *obtusifolius* not only in its overall larger dimensions, but in lacking stem elongation, a distichous leaf arrangement, and coriaceous-thickened leaves. Normal var. *obtusifolius* (*Huber* 11524) has been collected from the same locality.

### ***Rondonanthus capillaceus* (Klotzsch ex Koern.)**

Hensold & Giulietti, comb. nov. *Paepalanthus capillaceus* Klotzsch ex Koern. in C. Martius, Fl. Bras. 3(1): 415, t. 53, fig. II. 1863. *Dupatya capillacea* (Klotzsch ex Koern.) Kuntze, Revis. Gen. Pl. 2: 745. 1891. TYPE: Guyana: savannas of Mount Roraima and Humiridia, April–May, *Schomburgk* 1222 (holotype, B not seen). Figure 2.



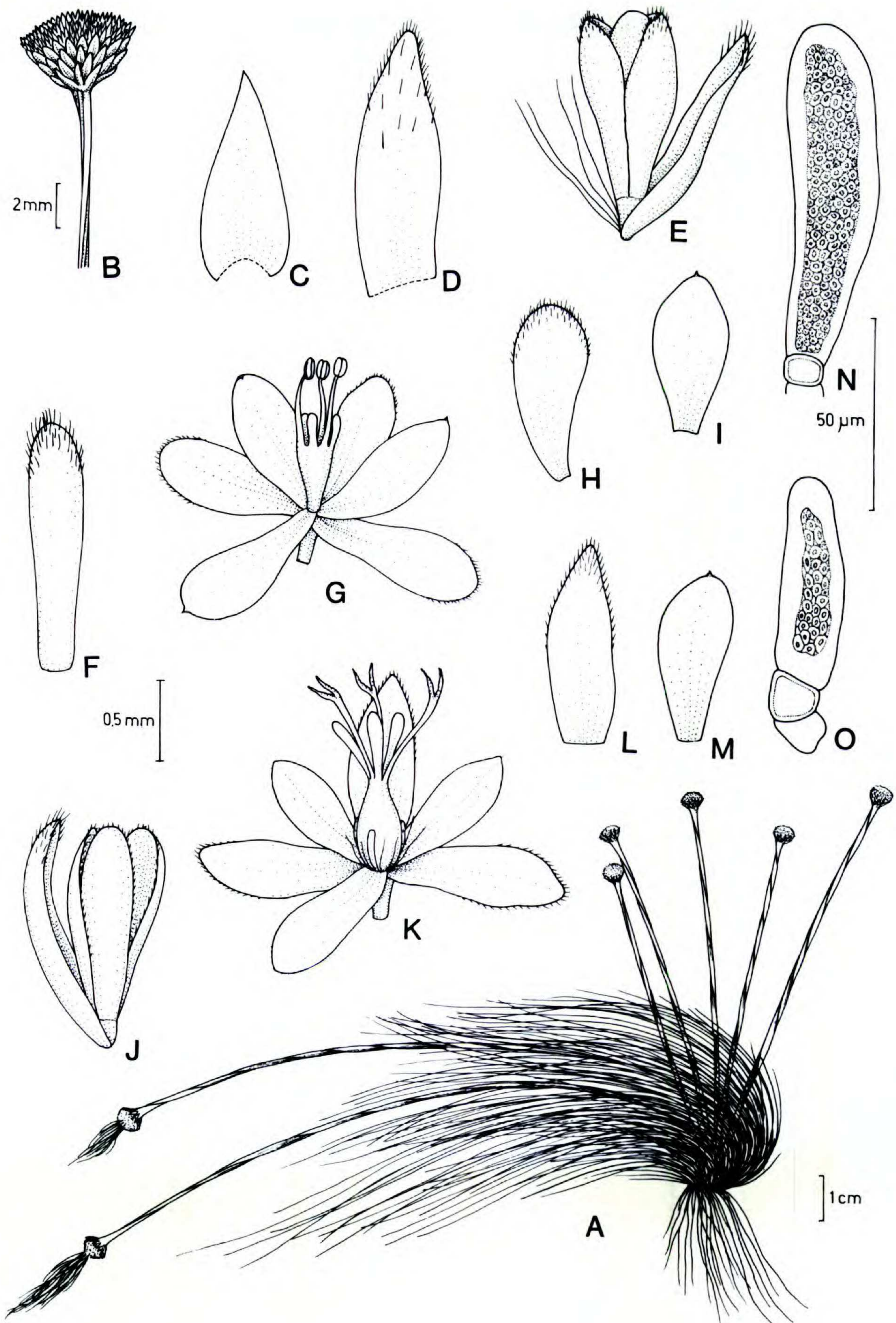


FIGURE 2. *Rondonanthus capillaceus* (Klotzsch ex Koern.) Hensold & Giuliatti (*R. Kral* 72131 MO).—A. Habit.—B. Inflorescence.—C, D. Involucral bracts, lower and upper. E–I. Staminate flower.—E. Whole flower, with floral bract.—F. Floral bract.—G. Flower with perianth spread open.—H. Sepal, abaxial view.—I. Petal. J–M. Pistillate flower.—J. Flower with bract.—K. Flower with perianth spread open.—L. Sepal, abaxial view.—M. Petal.—N, O. Trichomes of floral bract apex.

*Paepalanthus hippotrichophyllus* Herzog, Feddes Rept. Spec. Nov. Regni Veg. 29: 208. 1931. TYPE: Brazil. Amapá: Igarapé Crê-cru of the Rio Oyapock, Luetzelburg 21408 (holotype, M).

*Paepalanthus capillaceus* var. *proliferus* Gleason, Bull. Torrey Bot. Club 58: 328. 1931. *Paepalanthus capillaceus* forma *proliferus* (Gleason) Mold., Phytologia 44: 384. 1979. TYPE: Venezuela. Amazonas: Cerro Duida, Central Camp, 4,800 ft., Tate 552 (holotype, NY).

*Paepalanthus capillaceus* var. *spiralis* Mold., Mem. New York Bot. Gard. 9: 279. 1957. TYPE: Guyana. Upper Mazaruni River, Karaurieng River, Maipuri Falls, 1,250 m, Maguire & Fanshawe 32292 (holotype, NY; isotype, M). Note: This taxon, distinguished by its strongly spiral-twisted leaves, is known only from the type locality. Though it may be valid as a variety, it is here regarded conservatively as a synonym.

Plants short-stemmed aquatic perennials, the vegetative portions fully submerged and inflorescences mostly emergent and erect. Main roots abundant, ca. 0.5–1.0 mm diam., much-branched, gray-brown, contorted. Stems up to 7 cm long and 15 mm diam., leafy only near the apex, but the lower portions covered by persistent roots and leaf bases, woolly with brownish hairs. Leaves spirally arranged, pale green to blackish, (2.5–)7–30 cm long, 0.2–0.4 mm wide, the base slightly dilated, ephemerally woolly, coarsely filiform-setaceous, sometimes corkscrew-twisted, the tips acute but usually broken off, glabrous (though often with sand particles and algae adhering in dried material), traversed by a single central vein surrounded by mesophyll (Ruhland, 1903). Inflorescences numerous, synchronous, commonly numbering 10 or more. Peduncle sheaths 3–5 cm long, strongly twisted, glabrous, the apex acuminate, scarious, often lacerate. Peduncles (5.5–)9.0–20.0 cm long, 3-costate or apparently 6-costate by collapse of the centers of the main ribs, glabrous. Capitula 3–5 mm diam., depressed-turbinate to depressed-hemispheric at maturity, sometimes vegetatively proliferating from the center. Involucral bracts in ca. 4 series, both the outer and inner narrowly triangular, subacute to commonly obtuse, erect, the outer ca. 1.1–1.4 mm long, 0.5–0.7 mm wide, the inner 1.9–2.1 mm long, 0.5–0.7 mm wide, about equaling the head; all pale gold-brown to castaneous or nearly black, fleshy or coriaceous-thickened especially toward the base, the margins of at least the inner bracts  $\pm$  pellucid, shredding with age; glabrous or the inner bracts short-ciliate along distal margins. Floral bracts shorter than or about equaling the flowers, spatulate, obtuse, strongly keeled and somewhat cucullate at apex, cream-colored to pale brown, the apex hirsute abaxially with short subclavate hairs. *Staminate*

*flowers*. Pedicels ca. 0.3–0.5 mm long. Sepals obovate to spatulate, obtuse to rounded, concave, somewhat fleshy, 1.1–1.4 mm long, 0.45–0.6 mm wide, cream-colored to pale gray-brown, ciliate and short-hairy abaxially toward apex. Corolla of 3 separate petals (these separate from earliest visible stage of development), inserted at the base of the androphore (intercalary prolongation of the floral axis above the calyx), or at variable distances above the base, but usually below the insertion of the filaments and pistillodes; the androphore 0.1–0.5 mm long, the petals 1.1–1.5 mm long, 0.4–0.7 mm wide, obtrullate to obovate, rounded toward apex and abruptly apiculate, glabrous. Stamens with filaments 0.7–1.2 mm long, usually inserted at apex of androphore, though occasionally one or more inserted at base, included, the anthers ca. 0.15–0.2 mm long. *Pistillate flowers*. Pedicels 0.2–0.4 mm long. Sepals ovate to elliptic, concave, acute to obtuse, 1.2–1.5 mm long, 0.5–0.8 mm wide, colored as in staminate flowers, short-ciliate from middle to apex and short-hairy abaxially in this region, coriaceous-thickening at maturity, especially at base and sometimes throughout. Petals free, spatulate, usually acute or apiculate, 1.2–1.6 mm long, 0.4–0.6 mm wide, glabrous. Staminodes firm, linear to somewhat broad and nearly scalelike, 0.2–0.6(–1.4) mm long. Ovary with a few scattered hairs at base, 0.4–0.7 mm long, the style 0.1–0.4 mm long, the appendages 0.4–0.5 mm long, the stalk thick, the papillose portion orange-brown, darker than the stalk, the style branches diverging at the same level as the appendages, 0.7–0.9 mm long, bifid half to nearly all their length. Floral trichomes clavate and thick-walled with dense granular thickening of the internal wall.

*Phenology*. Collected in flower year-round.

*Habitat and distribution*. Adhering to rocks of streambeds in rapidly flowing water, 100–1,600 m. Venezuela. Amazonas: Cerros Duida and Marahuaca south to Neblina; Bolívar: Gran Sabana. Guyana: Upper Mazaruni River and Kaieteur Plateau. Brazil. Amazonas: Serra Aracá; Amapá: Rio Oyapock (Oiapoque).

*Additional specimens examined*. VENEZUELA. AMAZONAS: Cerro Duida, Fariñas et al. 420 (NY), Maguire & Maguire 29153 (MO, NY), Maguire et al. 29611 (NY); Tillett et al. 751-82 (NY); Cerro Marahuaca, Steyermark & Holst 130470 (MO); Cerro Aracuni, Liesner & Carnevali 22308 (MO), Wurdack & Adderley 43602 (NY); base of Cerro Neblina, Davidse & Miller 27038 (MO), Gentry & Stein 46937 (MO), Liesner 15737 (MO); Liesner 16653 (MO). BOLÍVAR: Canaima, Schnee 1745 (MO); Río Yuné, ESE of Churitepui, Huber 9764 (MO); headwaters of Río Venamo,

NW of Cerro Venamo, *Steyermark & Nilsson 16* (NY); Salto El Danto, *Knapp & Mallet 6711* (MO, NY), *Holst et al. 2117* (MO); Salto el Torón, *Thomas 2529* (NY); W of Sororopán-tepui, *Steyermark 60208* (F); Kavanayén, *Kral 70411* (MO), *Moore et al. 9836* (NY); upper Río Apongua, NW of Parupá, *Kral 72046* (MO); Río Apongua, *Trujillo 11599* (NY); 10 km SW of Karaurín-tepui, *Liesner 23486* (MO); Río Kamá, *Steyermark & Liesner 127619* (MO); Río Cauí, *Luteyn et al. 6323* (F, MO); Salto Yuruani, *Kral 70570* (MO), *Kral 72131* (MO). GUYANA. Upper Mazaruni, Utschi River, *Tillett & Tillett 45793* (MO); Upper Mazaruni, Kamarang River, Mt. Aymatoi, *Maas et al. 5731* (MO); Kaieteur Plateau, *Maguire & Fanshawe 23243* (MO). BRAZIL. AMAZONAS: Serra Aracá, *Prance et al. 29150* (MO).

*Rondonanthus capillaceus* is distinguished from all other species of the genus by its aquatic habit and filiform-setaceous leaves exceeding the peduncles. Its flowers differ from those of other species in several respects. The perianths lack black pigmentation and are short-hairy at the apex rather than long-ciliate. The granular ornamentation of the trichome internal wall is also exceptional and similar to that found in *Paepalanthus*. In the staminate flowers, an androphore is present, and the petals are usually free from the earliest stages of development.

It is here placed in *Rondonanthus* because of similarities in root and peduncle sheath morphology and involucre bract shape, and because of the presence of long linear staminodes in most material. (These are small and scalelike in a few populations.) The bifid stigmas in combination with long hairs at the base of the ovary also suggest *Rondonanthus*.

This species has the largest distribution of any in the genus, with a disjunct population in Amapá, Brazil. These plants, described by Herzog (1931) as *Paepalanthus hippotrichophyllus*, are mistakenly reported to have tubular corollas in the staminate flowers.

*Rondonanthus capillaceus* is highly convergent with *Leiostrix fluitans* (C. Martius) Ruhl. of Minas Gerais, Brazil, another submerged aquatic of rapidly flowing water. The species have similar vegetative morphology and both have free petals in both pistillate and staminate flowers, suggesting that this floral modification may be somehow at least incidentally correlated with adaptation as an aquatic. They are distinguished primarily by the structure of the gynoecium and by the presence or absence of staminodes.

***Rondonanthus caulescens*** (Mold.) Hensold & Giulietti, comb. et stat. nov. *Paepalanthus jauensis* var. *caulescens* Mold., *Phytologia* 44: 215. 1979. TYPE: Venezuela. Bolívar: Cumbre de Aprada-tepui, 2,460–2,500 m, 25

Feb. 1978, *Steyermark et al. 115893* (holotype, LL; isotypes, F, MO).

Plants short-stemmed, caespitose perennials. Main roots ca. 0.5 mm diam., sparingly branched, pale orange-brown. Stems 4–6 cm long at flowering, ca. 2–3 mm diam., leafy to the base, woolly with cream-colored hairs. Leaves spirally arranged, 3–4 cm long, 0.6–1.0 mm wide; the bases somewhat dilated, broadest below, scarious, densely woolly; the blades linear, sharply acute, rigid, glabrous, 3–5-veined, the veins of equal size. Inflorescences single per age class, the old ones often persistent on stem. Peduncle sheaths 4–5 cm long, twisted, glabrous, the apex sharply acute to acuminate, green, often lacerate with age. Peduncles 15–35 cm long, 3-costate, pubescent with retrorse malpighian hairs especially toward apex, and long filamentous hairs fringing the base of the capitulum. Capitula 7.5–10 mm diam., turbinate to hemispheric at maturity. Involucral bracts in 3 series, the outer narrowly triangular, acute, spreading, ca. 2.3–2.7 mm long, 0.5–0.8 mm wide at base, the inner bracts elliptic to oblanceolate, acuminate, erect, ca. 4.5 mm long, 1.3–1.4 mm wide, equaling the head or surpassing it slightly (up to 0.5 mm); the outer bracts gold-brown, often with some irregular blackish streaks, the inner mostly black with a paler tip and distal midvein; the outer and inner bracts ciliate to the base and also hirsute abaxially, the inner tufted at the apex. Floral bracts slightly exceeding the flowers, linear-oblanceolate, acuminate, creamy hyaline and flecked with black distally, tufted abaxially at apex. *Staminate flowers*. Pedicels 1.3–1.5 mm long. Sepals obovate-elliptic, acuminate, ca. 2.2–3.0 mm long, 0.8–1.0 mm wide, hyaline with black flecks, sometimes appearing gray except for pale base and apex, the apex tufted abaxially with divergent-ascending trichomes. Corolla connate into a 3-lobed tube, the androphore lacking, the tube ca. 2.3–2.8 mm long, the lobes triangular-obtuse, the upper margin ciliate, involute, and retracting the stamens after anthesis. Stamens with filaments adnate to corolla at base, included; anthers ca. 0.35 mm long. *Pistillate flowers*. Pedicels ca. 0.8 mm long. Sepals ovate-elliptic, concave, acuminate, 2.8–3.2 mm long, ca. 0.8–1.1 mm wide, cream-colored or slightly grayish, pubescent as in the staminate flowers, not observed in mature condition. Petals connate in distal half, the segments oblong, triangular-obtuse at apex, ca. 2.5–3.0 mm long, 0.5 mm wide, ciliate at upper margin and also pilose abaxially in submarginal bands. Staminodes linear, 0.6–0.9 mm long. Ovary ringed by hairs at base, 0.5

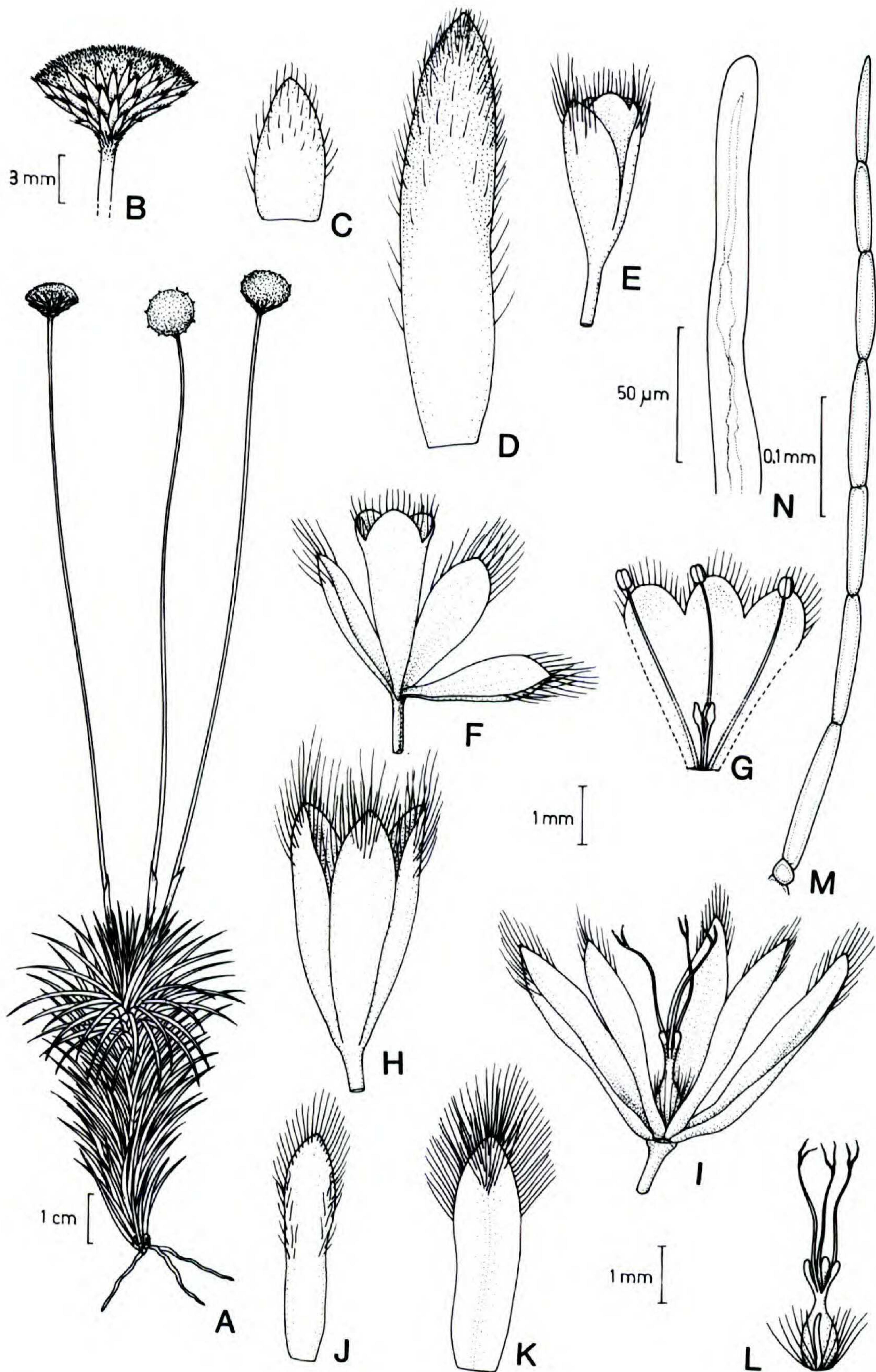


FIGURE 3. *Rondonanthus duidae* (Gleason) Hensold & Giulietti (Steyermark 58319 MO).—A. Habit.—B. Inflorescence.—C, D. Involucral bracts, lower and upper. E–G. Staminate flower.—E. Flower.—F. Flower with sepals spread apart.—G. Corolla, opened to show stamens and pistillodes. H–L. Pistillate flower.—H. Flower.—I. Flower with perianth spread apart.—J. Petal, adaxial view.—K. Sepal, abaxial view.—L. Gynoecium, shown with subtending hairs and a staminode.—M, N. Trichomes of floral bract apex.

mm long, the style 0.3 mm long, the appendages ca. 0.4 mm long, the stalk rather thick, the papillose portion pale orange, the style branches diverging slightly above the appendages, 2.5 mm

long, bifid. Floral trichomes subacute, lacking granular thickening of the internal wall.

*Phenology.* Collected in flower in February.

*Habitat and distribution.* Known only from the type; no habitat information given.

This species appears more similar to *R. acopanensis* of the Chimantá Massif than to "*P. jauensis*" (here included in *R. duidae*), with which it occurs sympatrically at Aprada-tepui, and of which it was originally described as a variety. It is allied with *R. acopanensis* by the acuminate, colorless apices of the involucre bracts and perianth, and by the more densely woolly leaf bases which are broadest at the base.

***Rondonanthus duidae*** (Gleason) Hensold & Giulietti, comb. nov. *Paepalanthus duidae* Gleason, Bull. Torrey Bot. Club 58: 329. 1931. TYPE: Venezuela. Amazonas: summit of Mount Duida, 5,500–6,000 ft., *Tate 456* (holotype, NY). Figure 3.

*Syngonanthus phelpsae* var. *pilosus* Mold., Mem. New York Bot. Gard. 9: 282. 1957. TYPE: Venezuela. Amazonas: Cerro de la Neblina, W escarpment, 1,850–1,900 m, *Maguire et al. 37308* (holotype, NY; isotype, F). Syn. nov.

*Syngonanthus phelpsae* var. *viridis* Mold., Phytologia 22: 126. 1971. TYPE: Venezuela. Amazonas: Cerro de la Neblina, Planicie de Zuloaga, 2,300 m, *Steyermark 103840* (holotype, NY; isotype, LL). Syn. nov.

*Paepalanthus jauensis* Mold., Mem. New York Bot. Gard. 23: 850, fig. 5. 1972. TYPE: Venezuela. Bolívar: Cerro Jaua, cumbre de la porción centro-oeste, 1,900–2,100 m, *Steyermark 97906* (holotype, LL). Syn. nov.

*Paepalanthus duidae* var. *parvifolius* Mold., Phytologia 54: 121. 1983. TYPE: Venezuela. Amazonas: Cerro Marahuaca, 2,750 m, *Tillett et al. 752-349* (holotype, NY). Syn. nov.

Plants rosulate or short-stemmed caespitose perennials, rarely branching above the base. Main roots 0.5–1.0 mm diam., sparingly branched, cream to pale orange. Stems up to 10 cm long, occasionally up to 40 cm long but then sterile, ca. 2–5 mm diam., densely leafy to the base, woolly with light brown hairs. Leaves spirally arranged, 1.5–15 cm long, 0.3–1.5 mm wide; the base slightly dilated just below the blade and then usually constricted proximally, pubescent with long matted feltlike hairs as on the stem; the blades linear to acicular, usually sharp-cuspidate, subterete and rigid to flat and chartaceous, glabrous to densely pubescent with retrorse malpighian hairs, usually with the midvein on the lower surface prominently thickened in contrast to the two narrow lateral veins (occasionally leaves merely acute and midvein similar in thickness to laterals). Inflorescences about 1–4 per age class, the old ones often persistent on stem. Peduncle sheaths 2–6.5 cm long, twisted,

pubescent like the leaves, the apex acuminate, scarious. Peduncles (6–)11–39 cm long, 6-costate, pubescent with retrorse malpighian hairs to nearly glabrous, usually with long filamentous hairs fringing the base of the capitulum. Capitula 6–14 mm diam., hemispheric at maturity. Involucral bracts in 4–6 series, the outer ovate to narrowly triangular or lanceolate, subacute, often recurved, 0.5–4.0 mm long, 0.4–1.2 mm wide at base, the inner bracts truly oblanceolate though appearing lance-linear to lanceolate in their exposed portions, tapered to an acute or narrowly rounded apex, erect or somewhat spreading, 2.5–8.5 mm long, 0.6–1.5 mm wide, often surpassing the head, sometimes by as much as 3–4 mm; variable in color, ranging from uniform deep brown with a dark reddish midvein to blackened only along the distal margins of the inner bracts with the outer bracts and medial areas of the inner bracts a strongly contrasting pale gold; glabrous or often ciliate, and then often hirsute abaxially (rarely also adaxially) at apex. Floral bracts commonly equaling or slightly surpassed by the flowers, linear to linear-oblanceolate, acute to subacute, blackened distally, bearded with long hairs abaxially at apex. *Staminate flowers.* Pedicels 0.5–1.5 mm long. Sepals broadly spatulate, rounded to acute, and sometimes the upper margin lacerate, 1.5–2.7 mm long, 0.6–1.2 mm wide, uniformly blackened distally, white below, rarely dark brown distally, grading into a lighter brown (Cerro Jaua and Sarisariñama), bearded abaxially with long erect trichomes. Corolla connate into a 3-lobed tube, or the petals very rarely free from each other, the androphore lacking, the tube 2.0–3.0 mm long, the lobes rounded and sometimes (Aprada-tepui) the sinuses rather deep, almost equaling the tube in length, the upper margin and abaxial lobe apices densely pilose, involute after anthesis. Stamens with filaments adnate to corolla at base, usually exsert; anthers ca. 0.2–0.3 mm long. *Pistillate flowers.* Pedicels 0.4–1.5 mm long. Sepals broadly elliptic to ovate-elliptic, concave, acute, 2.0–4.2 mm long, 1.0–1.5 mm wide, cream-colored or sometimes pigmented as in staminate flowers toward the apex though usually much less so, ciliate for most of their length and bearded at the apex as in the staminate flowers, thickening at base at maturity. Petals mostly free, rarely briefly connate distally, oblong to subspatulate, obtuse to acute, 2.0–3.5 mm long, 0.5–1.5 mm wide, densely ciliate at upper margin and frequently also pilose abaxially at apex or in submarginal bands. Staminodes linear, 0.2–2.0 mm long. Ovary ringed by hairs at base, 0.5–0.8 mm long, the style 0.2–0.6 mm long, the appendages ca. 0.6–1.0 mm long, the stalk usually

long and narrow, up to  $\frac{2}{3}$  the total length, the papillose portion white, sometimes collapsing after anthesis and appearing nearly filiform, the style branches diverging slightly above the appendages, 1.5–2.5 mm long, bifid, though in many cases the two segments cohering. Floral trichomes subacute to rounded, lacking granular thickenings of the internal wall.

*Phenology.* Collected in flower mostly from September to February, rarely in March and June.

*Habitat and distribution.* Locally abundant on open plateaus with shallow, rocky, wet soils, at 1,600–2,800 m. Venezuela. Amazonas: summits of Cerros Marahuaca, Duida, and Neblina; Bolívar: summits of Cerros Jaua, Sarisariñama, and Aprada-tepui.

*Additional specimens examined.* VENEZUELA. AMAZONAS: summit of Cerro Duida, *Steyermark* 58319 (F, MO, NY, VEN), *Steyermark* 58361 (F, NY); Cerro Duida, summit of Peak 7, *Tate* 625 (NY); Cerro Duida, Caño Sapó, *Tate* 691 (NY); Cerro Marahuaca, SE section, *Maguire et al.* 65637 (MO, NY), *Maguire et al.* 65638 (MO, NY, VEN), *Maguire et al.* 65639 (MO, NY); Cerro Marahuaca, NW section, *Steyermark et al.* 124366 (MO, NY), *Steyermark et al.* 124469 (NY); Cerro Marahuaca, extreme SE section, *Steyermark* 129109 (LL, MO); Cerro Marahuaca, extreme NE section, *Steyermark* 129191 (MO, VEN), *Steyermark & Delascio* 129247 (LL); Cerro Marahuaca, central part of the SE Meseta, *Steyermark* 129475 (LL, MO); Cerro Marahuaca-huha, *Steyermark* 125932 (LL, VEN); Cerro Marahuaca-Fhuif, *Steyermark et al.* 126099 (LL); Cerro Marahuaca-Atuhua-Shiho (SW of Cerro Marahuaca), *Steyermark* 126295 (LL, VEN); Cerro de la Neblina, Río Yatua, *Maguire et al.* 36930 (NY), *Maguire* 37123 (NY, VEN), *Maguire et al.* 42261 (F, NY, VEN), *Maguire et al.* 42279 (F, NY, VEN); NW plateau, *Liesner* 16028 (MO), *Liesner* 16046 (MO); Planicie de Zuloaga, Río Titirico, *Steyermark* 103878 (NY), *Steyermark* 103920 (NY). BOLÍVAR: Macizo de Sarisariñama, *Fernandez* 4753 (MO, PORT); Aprada-tepui, *Steyermark* 115885 (F, MO, VEN); S section, 30 km E of Urimán, *Huber* 9539 (MO).

The amount of variation in *Rondonanthus duidae* is very high, with some of the variation geographically distributed, and some probably environmental, such as leaf length and width, which can vary considerably within a single population. Involucral bract color varies geographically. The plants of Cerro Marahuaca, Aprada-tepui, and some of Cerro de la Neblina have uniformly black involucre, while plants of Duida and some of Neblina have highly contrasting gold and black or almost entirely gold bracts. Plants of Jaua and Sarisariñama have more rounded bract apices, and lack characteristic black color to bracts and perianth, having a dull brown color instead. Plants of Aprada-tepui are distinguished by very long black invo-

lucral bracts and by *Syngonanthus*-like fusion of the petals of the pistillate flower corolla.

This species is closely related to *Rondonanthus roraimae*, from which it can only be satisfactorily distinguished by reference to flower morphology. In general, the leaves of *R. duidae* also differ from those of *R. roraimae* by the prominent midvein and aristate tip, but this character is lacking in some collections (Aprada-tepui and some of Neblina).

*Rondonanthus duidae* is also habitually similar to *S. duidae* Mold., with which it is sympatric. These species are so similar in general aspect that two collections of *R. duidae* have been described as new varieties of *S. phelpsae* (now placed in *S. duidae*). At Neblina some plants look intermediate with *S. duidae*, with rather short, unevenly blackened involucral bracts, with the sepal apices sharply acute-lacerate and bearded below the apex, but not at the apex (as in *S. duidae*), the corolla of the staminate flower developing rather irregularly, and the gynoeceium intermediate with a rather long common style and style branches apparently fine and simple, not bifid. This is particularly true of the type of *S. phelpsae* var. *pilosus* Mold. It is possible that hybridization is occurring at Neblina, although *S. duidae* has never been collected south of Cerro Aracamuni.

Another possible hybrid requiring more study is the type of *Paepalanthus fraternus* var. *radiatus* Mold. (*Phytologia* 49: 383–386. 1981) from Cerro Marahuaca. The leaves of this plant are dull green and rounded at the apex rather like the sympatric species *Paepalanthus parvicephalus* (Mold.) Hensold, but have a cartilaginous texture, and are rosulate. The peduncles are of variable lengths, and the lanceolate radiating involucral bracts and soft heads which flatten upon pressing suggest *R. duidae*. The flowers are intermediate between the two taxa, with some developmental irregularities, particularly in the gynoeceium.

***Rondonanthus flabelliformis*** (Mold.) Hensold & Giuliatti, comb. nov. *Wurdackia flabelliformis* Mold., Mem. New York Bot. Gard. 9: 413. 1957. TYPE: Venezuela. Bolívar, Chimantá Massif, Torono-tepui, 2,165–2,180 m, *Steyermark & Wurdack* 671 (holotype, NY; isotypes, F, K). Figure 4.

Plants caulescent perennials. Main roots ca. 1–1.5 mm diam., sparingly branched, pale orange-brown. Stems up to 16 cm long, densely leafy to the base, woolly with grayish hairs. Leaves distichous, 9–10 cm long, 5–8 mm wide; the bases

slightly dilated linear or broader below, densely woolly with matted whitish hairs; the blades ligulate-falcate, obtuse to rounded, rigid, shiny, glabrous, ca. 30-veined, the veins of equal size, the margins pale and slightly revolute. Inflorescences up to 4 per age class. Peduncle sheaths ca. 6 cm long, not twisted, glabrous, the apex acute, green or somewhat scarious. Peduncles 13–16 cm long, 7–8-costate, pubescent with retrorse malpighian hairs between costae, and long filamentous hairs fringing the base of the capitulum. Capitula 15–19 mm diam., hemispheric to subglobose at maturity. Involucral bracts in 5 series, the outer triangular, acute, ca. 4 mm long, ca. 1.0 mm wide at base, the inner bracts spatulate, rounded and minutely apiculate, ca. 6 mm long, 1.5 mm wide, about equaling the head; the outer bracts gold-brown, coriaceous, the inner black, chartaceous, except for the gold-brown midvein; the outer bracts glabrous, the inner bearded abaxially at the apex, glabrate with age. Floral bracts about equaling the flowers, spatulate, obtuse, the distal half blackened, bearded abaxially at apex. *Staminate flowers*. Pedicels not measured. Sepals oblong-obovate, rounded and apiculate, ca. 2.7–2.9 mm long, ca. 0.7–0.8 mm wide, blackened distally, bearded abaxially with long, erect trichomes. Corolla connate into a 3-lobed tube at first, the segments later separating at least at the base, the androphore lacking; the tube 3.3 mm long, the lobes rounded, the upper margin and abaxial lobe apices ciliate-pilose, involute after anthesis. Stamens with filaments adnate to corolla, included; anthers ca. 0.3–0.35 mm long. *Bisexual flowers*. Pedicels ca. 2 mm long. Sepals ovate, concave, obtuse, ca. 4 mm long, 1.3 mm wide, cream-colored, bearded as in the staminate flowers, thickening at base at maturity. Petals connate into a tube except at base, the segments spatulate,  $\pm$  rounded at apex, ca. 3.5 mm long, 1.0–1.2 mm wide, densely long-ciliate at upper margin. Stamens present, opposite the petals, similar to those of the staminate flowers, but with the filaments slightly shorter. Ovary with no hairs at the base, ca. 0.5 mm long, the style 0–0.3 mm long, the appendages ca. 0.5 mm long, the stalk thick, the papillose portion brownish, the style branches diverging slightly above the appendages, ca. 2 mm long, conspicuously bifid. Floral trichomes subacute to rounded, lacking granular thickenings of the internal wall.

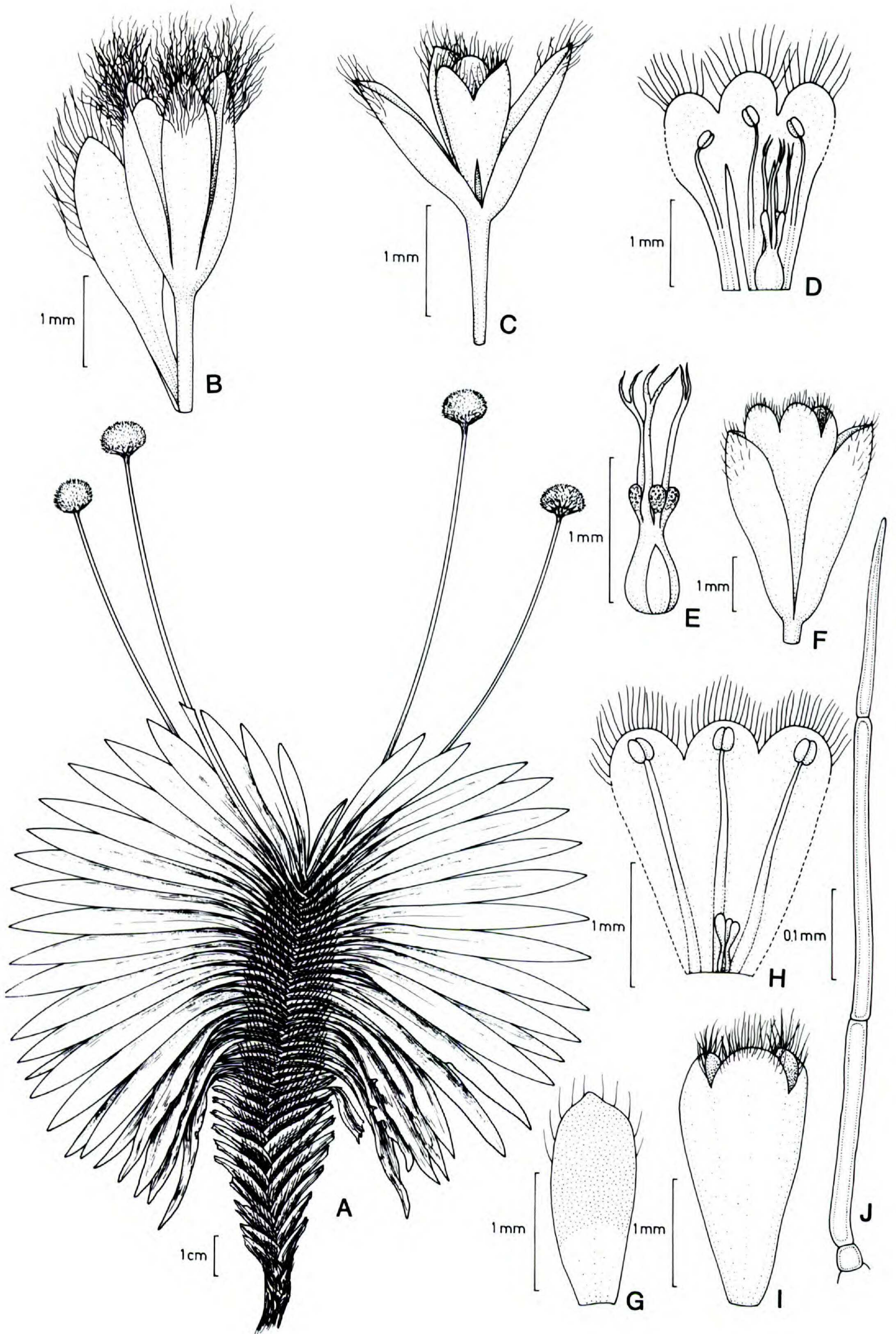
*Phenology*. Collected in flower in February.

*Habitat and distribution*. Known only from the type, reported as locally frequent in a *zanjon* (large crevice), in moist places among rocks.

*Rondonanthus flabelliformis* is clearly closely related to *R. acopanensis*, differing in the persistence of the leaves along the stem, in the very large size of the leaves and capitula, and in the occurrence of stamens in the morphologically pistillate flowers. It would be of great interest to determine the relationship between these two species. It is possible that *R. flabelliformis* has been derived from *R. acopanensis* by macromutation, a suspicion supported by the occurrence in the latter species of discontinuous size classes. Alternatively, it may be postulated as a primitive relict, with the persistent leaves and bisexual flowers representing an ancestral condition.

***Rondonanthus roraimae*** (Oliver) Herzog, Feddes Repert. Spec. Nov. Regni Veg. 29: 210. 1931. *Paepalanthus roraimae* Oliver, Trans. Linn. Soc. London, Bot. 2: 286. 1887. TYPE: Guyana. Mount Roraima, 15 Dec. 1884, Thurn 294 (holotype, K). Figure 5.

Plants rosulate or caulescent cespitose perennials. Main roots ca. 0.3–0.7 mm diam., sparingly branched, cream to pale orange. Stems up to 10 cm long, 2–3 mm diam., leafy to the base, woolly with light brown hairs. Leaves spirally arranged, 1.5–4 cm long, 0.5–1.3 mm wide; the base slightly dilated just below the blade and then usually constricted below, pubescent with long matted feltlike hairs as on the stem; the blades linear to acicular, the apex rounded or bluntly cuspidate, subterete and rigid to flat and chartaceous, glabrous or sparingly pubescent with retrorse malpighian hairs, especially abaxially, and then usually glabrate, 3-veined, the veins of equal size. Inflorescences 1(–5) per age class. Peduncle sheaths 3–4(–6) cm long, twisted, pubescent like leaves, the apex usually erose-toothed, scarious, eventually lacerate. Peduncles 5–28 cm long, 6–10-costate, pubescent with retrorse malpighian hairs to nearly glabrate, usually with long filamentous hairs fringing the base of the capitulum. Capitula 8–13 mm diam., hemispheric at maturity. Involucral bracts in 4–5 series, the outer ovate-triangular to lanceolate, subacute, often recurved, 2.3–3.7 mm long, 0.8–1.2 mm wide at base, the inner bracts lanceolate to oblanceolate and then appearing lance-linear to lanceolate in their exposed portions, tapered to an acute or subacute apex, erect or somewhat spreading, 4.5–7.0 mm long, 1.0–1.5 mm wide, surpassing the head by 1–2.5 mm; the outer bracts mostly castaneous, or sometimes fuscous along the margins, progressively darker above, the innermost bracts commonly deep fuscous with only the mid-





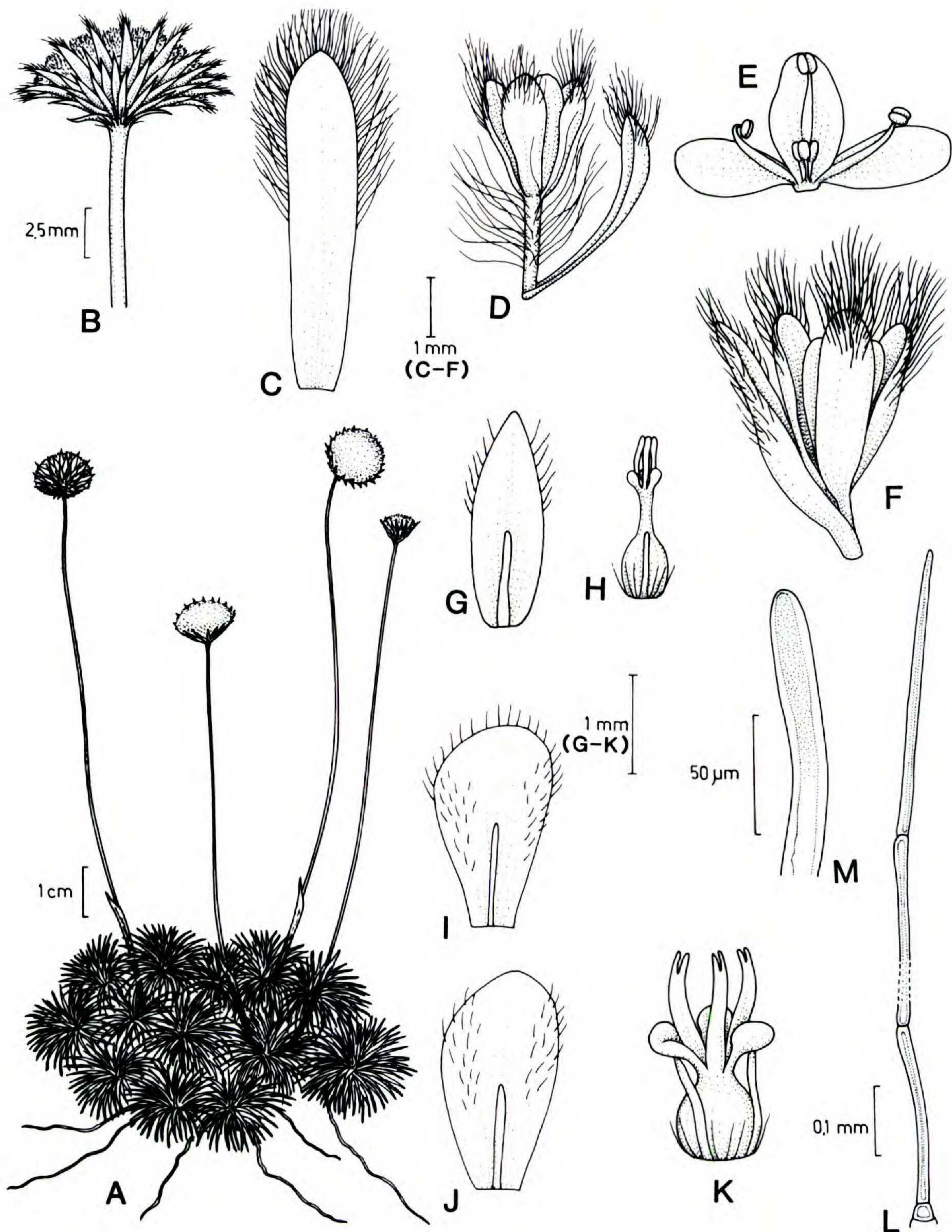


FIGURE 5. *Rondonanthus roraimae* (Oliver) Herzog (*Liesner 23239 MO*, unless stated otherwise).—A. Habit.—B. Inflorescence.—C. Involucral bract, adaxial view. D, E. Staminate flower.—D. Flower with bract.—E. Corolla, opened, with stamens and pistillodes. F–K. Pistillate flower.—F. Flower with bract.—G. Petal, adaxial, with staminodes.—H. Gynoecium, with staminodes and subtending hairs. I–K. Large-flowered morph (*Aymard 2480 PORT*).—I, J. Petals with staminodes.—K. Gynoecium, with staminodes and hairs.—L, M. Trichomes of floral bract apex.

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FIGURE 4. *Rondonanthus flabelliformis* (Mold.) Hensold & Giulletti (*Steyermark & Wurdack 671 NY*).—A. Habit. B–E. Bisexual flower.—B. Flower.—C. Flower with sepals spread apart.—D. Corolla opened to show functional stamens and gynoecium.—E. Gynoecium. F–I. Staminate flower.—F. Flower (pedicel broken).—G. Sepal, adaxial view.—H. Corolla, opened to show stamens and pistillodes.—I. Corolla, entire.—J. Trichome of floral bract apex.

vein castaneous; usually densely and persistently ciliate, the inner also commonly hirsute abaxially along the margins, rarely tufted at apex, occasionally glabrate. Floral bracts commonly equaling the flowers, linear, acute to subacute, blackened distally, bearded abaxially with long hairs. *Staminate flowers*. Pedicels 1.0–2.5 mm long. Sepals broadly oblanceolate to obovate, rounded to acute, 1.5–2.5 mm long, 0.5–1.3 mm wide, uniformly blackened distally, white below, bearded abaxially with long erect trichomes. Corolla connate at first into a 3-lobed tube, but the segments separating before anthesis, the androphore lacking; the petal segments 1.9–2.5 mm long, 0.9–1.5 mm wide, obovate, rounded to subacute, glabrous. Stamens with filaments adnate to corolla at base, included; anthers ca. 0.3–0.4 mm long. *Pistillate flowers*. Pedicels 0.9–1.3 mm long. Sepals obovate to spatulate, concave, acute to obtuse, 1.5–2.1 mm long, 0.6–1.8 mm wide, of the same color and pubescence as in the staminate flowers, thickening at base at maturity. Petals free,  $\pm$  obovate, rounded to apiculate, 1.5–2.1 mm long, 0.6–1.2 mm wide, sparingly ciliate along lateral margins below apex, and frequently also pilose abaxially in submarginal bands. Staminodes linear, 0.5–1.2 mm long. Ovary ringed by hairs at base, 0.5–0.7 mm long, the style ca. 0.3 mm long, the appendages ca. 0.4–0.5 mm long, the stalk narrow, the papillose portion white, the style branches diverging slightly above the appendages, ca. 1.0–1.2 mm long, bifid though the two segments often failing to separate. Floral trichomes rounded to clavate, lacking granular thickenings of the internal wall, though sometimes lightly flecked.

*Phenology*. Collected in flower mostly June to September, occasionally April and March.

*Habitat and distribution*. In open rocky or boggy, often partially inundated areas over thin soils or rock, 2,300–2,800 m. Venezuela. Bolívar: summits of Mount Roraima, Kukenán-tepui, Yuruani-tepui, and Ilú-tepui. Guyana: summit of Mount Roraima.

*Additional specimens examined*. VENEZUELA. BOLÍVAR: Ilú-tepui, NW sector (Tramén-tepui), *Huber 10065* (NY); Yuruani-tepui, *Huber 11813* (MO); Kukenán-tepui, *Huber & Alarcon 10526* (MO), *Liesner 23069* (MO); summit of Mount Roraima, *Aymard & Luteyn 2480* (NY, PORT), *Bechine 92* (MY), *Hernandez 1* (MY), *Steyermark 58799* (F, NY, VEN), *Steyermark 112438* (F, NY), *Steyermark 112608* (VEN). GUYANA. MAZARUNI-POTARO: summit of Mount Roraima, *Abbenetto 8* (K), *Connell & Quelch 660* (K, NY), *Liesner 23239* (MO), *Liesner 23316* (MO), *Luetzelburg 21605* (NY), *Quelch & Connell 102* (K, NY), *Quelch & Connell 315* (K), *Tate 372* (NY).

*Rondonanthus roraimae*, as the type of the genus, was originally described as dioecious and having free petals in both pistillate and staminate flowers. Though the trend to dioecy is pronounced, monoecious plants are occasionally found. In addition, petal fusion in staminate flowers is found to occur early in development, although in older, post-anthesis flowers, which are easier to dissect and interpret, the petals are invariably free.

The species, endemic to the Roraima formation of eastern Venezuela, is very similar to *R. duidae*, found to the west. *Rondonanthus roraimae* can be distinguished by the glabrous, ephemerally fused corolla segments of the staminate flowers, and also usually by leaf characters (see *R. duidae*). Other characters distinguishing *R. roraimae* are the included stamens with fleshy filaments and larger anthers, as well as the much shorter (but not narrower) petals, style branches, and appendages in the pistillate flowers. These characters, together with the more swollen floral trichome apices, all suggest polyploidy. (A similar suite of characters distinguishes the tetraploid *P. mollis* var. *itambeensis* Hensold from *P. mollis* Kunth var. *mollis*; Hensold, 1988). In addition, *R. roraimae* blooms earlier in the year than *R. duidae*.

#### EXCLUDED SPECIES

*Rondonanthus micropetalus* Mold., *Fieldiana*, Bot. 28: 126. 1951. TYPE: Venezuela. Bolívar: Mount Roraima, SW-facing side, *Steyermark 58777* (holotype, NY; isotype, F).

This species is an abnormal form of *Paepalanthus roraimensis*, with dwarf peduncles and abnormal floral development. In the material observed, the staminate corollas were abortive and underdeveloped, represented only by small lobes of tissue on the floral axis, which were apparently interpreted as free petals.

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